AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 103:103–117 (1997)

Fueguian Cranial Morphology: The Adaptation to a Cold, Harsh Environment

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KEY WORDS Tierra del Fuego; craniometry; nasal form; cold stress; human adaptation; Mongoloids

ABSTRACT Craniometric data from the three extinct tribes that inhabited Tierra del Fuego (Selk'nam, Yámana, and Kawéskar) were gathered following Howells's measurement technique. We studied 180 skulls preserved at thirteen different institutions. Analysis of variance (ANOVA) between groups showed that morphological similarities among Fueguian groups are far more important than some differences between marine (Yámana and Kawéskar) and terrestrial (Selk'nam) groups. A principal component analysis (PCA) generated from the correlation matrix shows that Fueguians fall as outliers with respect to the typical Mongoloid morphology. In addition, a UPGMA tree generated from a squared Euclidean distance matrix indicates that Fueguian groups have a morphological pattern that is very distinct from that of other present-day Amerindian groups, with the exception of the Eskimos. One of the variables that contributes substantially to the differentiation of Eskimos and Fueguians is the nasal height. This suggests that nasal morphology in both groups could be a response to adaptive pressures related to the cold environment. However, other morphological particularities of Fueguian skulls, such as craniofacial robustness and variables of craniofacial width, can be attributed to a large masticatory stress. As a whole, the morphological features of Fueguian groups can be regarded as a general adaptive response to a very harsh environment, along with the retention of some plesiomorphic features. Assuming that the initial entry in Tierra de Fuego took place around 10,000 years BP, before the disappearance of the last land bridges in the Magellan Straits, then this adaptation might have arisen in a relatively short period, hastened by the extreme environmental conditions. Am J Phys Anthropol 103:103–117, 1997. © 1997 Wiley-Liss, Inc.

Tierra del Fuego (the southern end of South America) is characterized by severe environmental conditions, to which the human groups that lived there adapted culturally and perhaps biologically. After the receding of the ice cap, around 16,000 BP, the descent of the sea level allowed terrestrial access to Isla Grande between 12,000 and 10,000 BP (Clapperton, 1992). Early human presence on Tierra del Fuego may correspond to this period (Massone, 1989), and human ocupation of Tierra del Fuego before 11,880 BP has been suggested (Stern, 1992). Lago Sofía Cave, north of the Magellan Straits, has been dated to 12,900 BP (Prieto, 1991), while the site of Tres Arroyos, in Isla Grande, has been dated between 10,420 and 10,280 BP (Massone, 1989). From about

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Received 26 February 1996; accepted 2 February 1997.

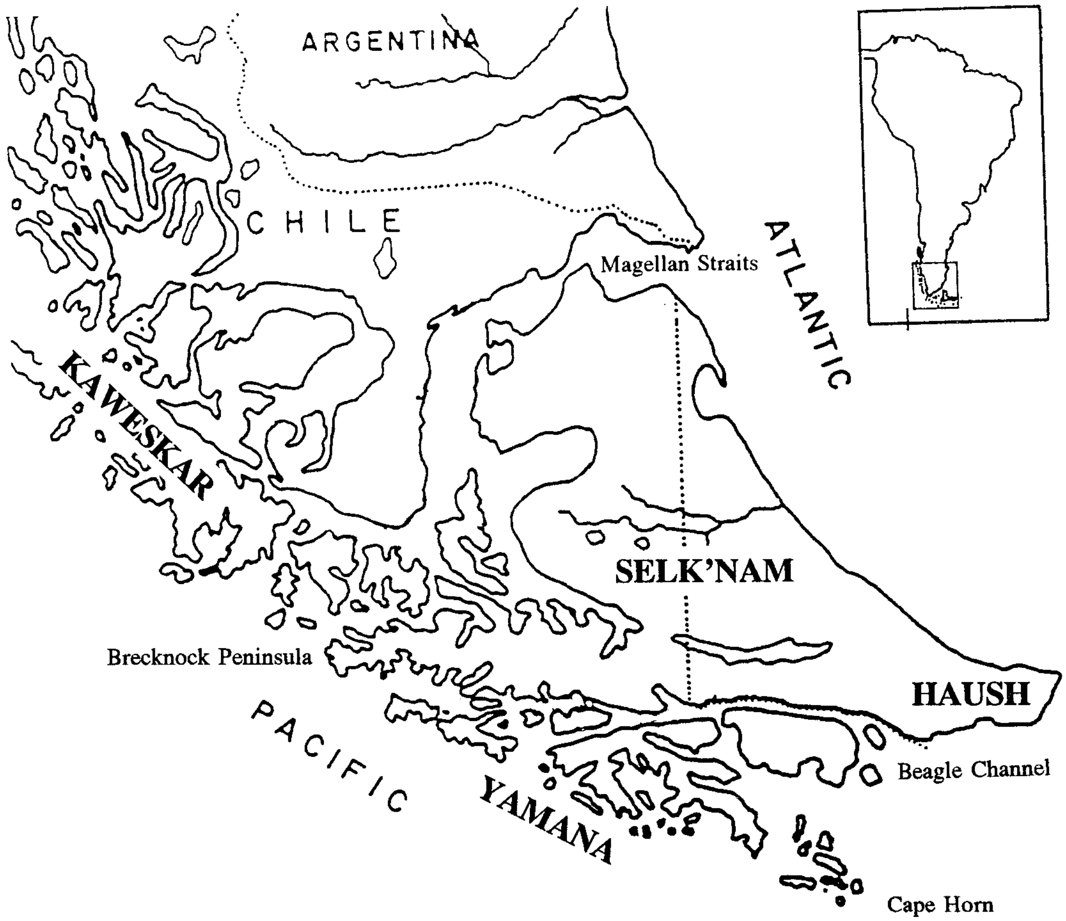

Fig. 1. Tierra de Fuego and the location of the four Fueguian tribes at the moment of the European contact (nineteenth century).

8,000 BP, with the disappearance of the last land bridges in the Magellan Straits, these populations remained almost isolated until European contact (Piana, 1984; Martinic, 1992). Archaeological evidence suggests a continuous human presence in the Beagle Channel area since at least 6,000 BP, with well-developed cultural adaptations to sea-food exploitation (Orquera et al., 1977; Piana, 1984).

Four hunter-gatherer groups inhabited Tierra del Fuego before European contact (Fig. 1). The Selk'nam or Ona were terrestrial hunter-gatherers who occupied most of Isla Grande. Their territory was limited to the south by the Darwin mountains. In the absence of appropriate building material for boats and because of the strong marine currents in the Magellan Straits, the Selk'nams were confined to Isla Grande. The Haush, a cultural subgroup of the Selk'nam, inhabited the south eastern part of Isla Grande and were greatly reduced in number even before European contact. The Yámana (or Yaghan) and the Kawéskar (Halakwulup or Alakaluf) were marine hunter-gatherers who lived in rudimentary canoes in the western archipelagos. The Yámana inhabited the coastal areas around the Beagle Channel, south to the Brecknock Peninsula, including Cape Horn. They are the only human group ever to have inhabited a region below 55° S. The Alakaluf lived on islands and channels of the Chilean Pacific

coast, from the Brecknock Peninsula to the Gulf of Penas. The two canoeing groups maintained occasional contacts with each other and also with the Patagons, who lived in the area north of the Magellan Straits. However, the geographically marginal position of the Fueguian aborigines with respect to the South American continent seems to have kept them apart from northern migratory movements.

Tierra del Fuego has a very cold, rainy, foggy, and windy climate (Xercavins, 1984; Endlicher and Santana, 1988), with perpetual snow and glaciers in the mountainous areas. In the Beagle Channel region the average temperature during the summer is 10°C, while during winter the temperature can reach −12°C, and daylight lasts only about 6 h. Isla Grande, located North of the Beagle Channel, has an even colder climate, with occasional temperatures of −20°C during the winter and very strong winds from the west. The constant winds dramatically increase the cold perceived by inducing wind chill. The combination of wind, cold, and rain makes Tierra del Fuego a harsh environment for humans. Despite these climatic conditions, the Fueguians lived almost naked and wore only small capes made from mammal skins, which did not cover their body. In addition, the Yámana and Kawéskar females frequently immersed themselves in the extremely cold water to collect molluscs (Gusinde, 1939; Martinic, 1992). The austerity of the Fueguian way of life and the harshness of the environment in which they lived impressed the early European visitors, who considered these aborigines representatives of an extremely "primitive" human group, (Cook, 1893; Darwin, 1962). Several anthropological studies have emphasized this image by documenting some of the striking characteristics of these aborigines, especially the unusual degree of cranial robustness, which was cited as a primitive indicator (Deniker, 1900; Biasutti, 1941; Vallois, 1948).

With the final extinction of Fueguian groups in the very first decades of the twentieth century, as a consequence of European colonization (Martinic, 1992; García-Moro et al., 1996), the cranial remains preserved at some institutions become an important source of anthropological information. The biological origin of Fueguian groups has become a subject of intense study, because they were the most austral peoples of the world and lived under extreme environmental conditions. Several studies attempted to describe the morphological characteristics and the intergroup relationships among Fueguian groups (Gusinde, 1939; Hernández, 1992; Varela et al., 1993–1994; Lalueza et al., in press). Recently, Lahr (1995), with a sample of 52 skulls, concluded that Fueguians show a very robust morphological pattern that is unlike what is seen in present-day Amerindian populations, and thus Fueguians might represent the morphology of a more generalized Mongoloid ancestral group. The same author found some similarities shared by Eskimos and Fueguians but attributed them to masticatory stress rather than cold adaptation, although Fueguians and Eskimos were the only American groups that lived in a subarctic or subantarctic environment.

In this study, cranial data on the three Fueguian groups have been collected, including 180 skulls (both female and male) and 24 commonly used craniometric measurements. A multivariate analysis including the human groups studied by Howells (1973, 1989) has been undertaken to determine whether the morphological particularities of Fueguian groups can be attributed to a response to different adaptive pressures or are simply the retention of plesiomorphic characteristics. In addition, the intragroup homogeneity of Fueguian ethnic populations has also been explored.

MATERIALS AND METHODS

The Fueguian sample

The sample from Tierra del Fuego includes 180 skulls preserved at 14 different institutions, nine of them in South America and five in Europe (Table 1). By groups, there are 80 Yámana (YAM) skulls, 25 Kawéskar (KAW), and 75 Selk'nam (SEL). There were only two skulls available that could be attributed with certainty to the Haush, and thus this interesting group could not be included in this study. The sample studied is the largest body of data ever

TABLE 1. Sample distribution and sample size of the studied Fueguian skulls

Institution	Sample size
Museo Etnográfico Ambrosetti, Buenos Aires	13
Museo de Historia Natural, La Plata	11
Museo Territorial, Ushuaia	7
Misión La Candelaria, Río Grande	9
Instituto de la Patagonia, Punta Arenas	19
Museo Mayorino Borgatello, Punta Arenas	6
Museo Municipal, Porvenir	6
Museo Martin Gusinde, Puerto Williams	8
Museo de Historia Natural, Santiago de Chile	24
Naturhistorisches Museum, Vienna	21
Istituto di Antropologia, Florence	16
La Sapienza, Rome	14
The Natural History Museum, London	15
Musée de l'Homme, Paris	11
Total	180

assembled for Fueguian populations (Gusinde (1939) collected 106 skulls).

It is difficult to assign some Fueguian skulls to a specific aboriginal group, as was found during the 1880s and later with the appearance of interethnic mating (Gusinde, 1939). However, more than 90% of the skulls of Fueguians from European collections have individual information stored in museum records and are assigned to a specific aboriginal group (García-Moro et al., 1988). The percentages are similar for collections in South America, although it cannot be excluded that some specimens could be misplaced.

The attribution of sex to the Fueguian skulls was achieved using standard traits of robustness and sexual dimorphism (Ferembach et al., 1986; Brothwell, 1981). General robusticity had to be considered carefully, especially for the Selk'nam group, in which females were considerably robust. However, information on sex was available for some individuals through the museum records.

Howells's series

To establish the morphological particularities of the three Fueguian groups, we also added the 28 craniometric series from Howells (1973, 1989) to the analyses (Table 2). The populations considered include cranial series from the world's major geographic regions: three from Europe (Norse (NOR), Zalavar (ZAL), and Berg [BER]), five from Africa (Egypt (EGY), Teita (TEI), Zulu (ZUL),

TABLE 2. Craniometric series included in the analyses[1]

Abbreviation	Population
NOR	Medieval Norse (Oslo)
ZAL	Medieval Hungary (Zalavar)
BER	Berg (Austria)
EGY	Egypt (twenty-sixth to thirtieth dynasties, Gizeh)
TEI	Teita (Kenya)
DOG	Dogon (Mali)
ZUL	Zulu (South Africa)
BUS	Bushmen (South Africa)
AND	Andaman Islands
AUS	Australian aborigines (Lake Alexandrina)
TAS	Tasmanian aborigines
TOL	Tolai (New Britain)
MOK	Mokapu (Oahu, Hawaii)
BUR	Buriat (Baikal, Siberia)
ESK	Eskimos (Greenland)
ARI	Arikara (South Dakota)
PER	Peru (Yaujos)
EAS	Easter Island
MOR	Moriori (Chatham Islands)
CAL	Santa Cruz (California)
HOK	Japan (Hokkaido)
KYU	Japan (Kyushu)
HAI	Chinese
TAI	Atayal (Taiwan)
PHI	Philippines
GUA	Guam
AIN	Japan (Ainu)
ANY	Anyang (China)
YAM	Yámana (Tierra del Fuego)
KAW	Kawéskar (Tierra del Fuego)
SEL	Selk'nam (Tierra del Fuego)

[1] Data from Howells (1973, 1989), except samples from Tierra del Fuego.

Dogon (DOG), and Bushmen [BUS]), six from the Pacific (Australians (AUS), Tasmanians (TAS), Tolai (TOL), Mokapu (MOK), Easter Island (EAS), and Moriori [MOR]), ten from Asia (Buriat (BUR), Andaman (AND), Japan (Ainu (AIN), Hokkaido (HOK), Kyushu [KYU]), Philippine (PHI), Chinese (HAI), Atayal (TAI), Guam (GUA), and Anyang [ANY]), and four from America (Eskimo (ESK), Arikara (ARI), Santa Cruz (CAL), and Peru [PER]). However, only Mongoloid groups were included in the multivariate analysis.

Skull measurements

The Fueguian skulls were measured following the methods of Howells (1973). Twenty-four common craniometric variables, mainly corresponding to the facial skeleton (Table 3), were considered for analysis.

Mean values of craniometric variables for the three Fueguian groups are displayed in Table 3, while the mean values for the other

TABLE 3. Craniometric data from the three Fueguian groups by sex[1]

		Yámana						Kawéskar						Selk'nam					
		Males			Females			Males			Females			Males			Females		
Variable definition	Howells's code	N	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.
Glabello-occipital length	GOL	41	186.32	5.37	37	178.16	5.29	15	188.33	3.98	10	179.40	3.75	50	191.26	6.19	24	185.08	6.70
Basion-nasion length	BNL	40	102.83	4.00	36	98.86	3.10	15	102.80	4.00	10	97.90	4.25	49	103.67	3.77	21	101.43	5.76
Basi-bregma height	BBH	39	135.97	4.86	34	131.68	3.98	15	137.93	5.32	10	129.50	2.68	49	136.55	4.65	21	132.24	5.57
Maximum Cranial breadth	XCB	41	142.88	3.80	36	138.50	4.83	15	142.13	3.93	10	137.60	4.72	50	143.10	4.82	21	140.10	4.72
Maximum Frontal breadth	XFB	40	116.85	4.52	35	112.40	5.21	15	115.20	4.72	10	111.20	5.25	47	116.21	4.76	22	114.18	4.26
Bizygomatic breadth	ZYB	35	143.26	4.02	31	133.16	4.76	15	141.00	7.07	10	131.30	4.16	46	143.46	5.55	20	137.70	5.55
Biauricular breadth	AUB	41	127.85	5.12	34	121.62	6.59	15	130.33	6.61	10	125.80	3.91	49	133.73	5.21	21	129.81	4.74
Biasterionic breadth	ASB	39	110.77	4.14	35	106.66	4.85	15	110.73	4.20	10	108.20	4.05	49	111.94	5.68	21	107.91	4.54
Basion-prostion length	BPL	40	101.80	4.92	34	98.88	4.58	15	101.87	5.71	10	96.90	5.65	48	101.33	3.55	21	98.76	5.23
Nasion-prostion height	NPH	42	73.24	3.49	36	68.44	4.16	15	75.00	4.33	9	68.44	3.47	48	76.50	4.88	23	74.00	4.96
Nasal height	NLH	42	54.02	3.59	35	51.11	3.49	15	56.07	2.71	10	51.00	2.91	48	55.38	3.41	23	54.04	2.82
Orbit height	OBH	42	35.74	2.05	36	34.64	2.21	15	35.80	2.08	10	35.10	2.02	49	35.45	2.15	23	35.39	1.97
Nasal breadth	NLB	42	24.86	1.51	35	23.54	1.87	15	24.40	1.76	9	23.56	2.40	47	25.30	1.84	23	24.39	1.23
External palate breadth	MAB	40	65.78	3.18	35	61.54	2.81	14	66.50	4.64	9	61.78	2.22	47	65.72	3.21	22	63.18	4.12
Bimaxillary breadth	ZMB	39	100.67	3.92	36	93.36	4.06	14	99.64	3.88	10	91.70	3.74	47	102.04	4.55	22	97.68	5.35
Bimaxillary subtense	SSS	38	26.18	3.29	36	24.28	2.12	14	25.21	2.75	10	24.20	3.11	46	26.85	3.04	22	25.36	3.08
Bifrontal breadth	FMB	40	101.73	3.52	35	96.91	3.67	14	103.00	3.53	10	96.30	3.27	49	104.84	3.34	22	100.09	5.33
Nasio-frontal subtense	NAS	40	16.58	1.82	35	15.14	2.24	14	16.86	3.53	10	14.80	2.10	49	17.08	2.33	22	16.09	2.84
Biorbital breadth	EKB	39	100.03	4.15	35	95.97	4.00	13	100.54	4.10	10	95.30	3.09	46	102.09	3.60	22	98.00	5.07
Inferior malar length	IML	41	39.00	3.44	35	37.63	3.23	15	38.73	3.20	10	36.20	2.25	46	39.74	2.34	19	36.95	3.34
Cheek height	WMH	42	25.14	2.02	36	22.61	2.00	15	25.20	1.90	10	21.50	1.35	49	25.80	2.29	22	25.59	7.04
Nasion-bregma chord	FRC	40	114.00	3.75	37	107.76	4.80	15	112.87	3.91	10	107.70	1.83	49	116.78	5.07	24	111.58	4.78
Bregma-lambda chord	PAC	40	110.68	5.56	37	107.95	5.17	14	115.57	5.68	10	107.30	5.20	49	114.31	5.87	24	111.83	6.02
Lambda-opisthion chord	OCC	38	99.34	6.00	35	96.20	4.41	14	97.57	4.52	10	94.40	3.57	46	97.15	3.72	23	95.78	5.49

[1] N, sample size; Mean, group mean; S.D., standard deviation.

series are published elsewhere (Howells, 1989). It should be noted that Fueguians present unusually high values for several variables, especially bizygomatic breadth (ZYB), glabello-occipital length (GOL), biauricular breadth (AUB), nasion-prosthion height (NPH), bifrontal breadth (FMB), cheek height (WMH), and nasal height (NLH).

Multivariate analysis

To evaluate the internal relationships and the morphological cohesion of the Fueguian sample, an analysis of variance (ANOVA) was undertaken by using the Scheffe multiple comparison procedure. When the ANOVA yielded statistically significant intergroup differences for a given variable, *t*-tests between each pair of populations were also generated to explore which groups account for these differences.

To characterize the relationships between populations, a principal components analysis was undertaken, considering only the Mongoloid populations from the Howells sample. This analysis allowed us to explore the morphological particularities of Fueguian groups with respect to the general Mongoloid pattern. The first three principal components were extracted from the correlation matrix, both for male and female samples, and no rotation of the factors was

performed. Each principal component is a linear combination of the observed variables that progressively account for smaller portions of the total variance. As the correlations between the factors and the variables are known, this kind of analysis can help to interpret morphological relations between populations.

A second multivariate analysis involved the characterization of the seven craniometric samples from the American continent (Eskimos, Arikara, Santa Cruz, Peru, Selk'nam, Yámana, and Kawéskar), with the generation of a squared Euclidean distance matrix from the whole craniometric data set. This is the most appropriate distance for measurements without scale changes (Dixon et al., 1983). The matrix was represented as a tree using the average linkage between groups algorithm (Sneath and Sokal, 1973). The UPGMA tree has been used simply as a way to represent average similarities between populations. The robustness of the branches was assessed through 100 random iterations of bootstrap from the original data set (Efron, 1982; Felsenstein, 1985). A cluster depending on the similarity between many craniometric variables should tend to form more frequently than others that depend on only a few variables, and thus the former will show high bootstrap values. However, it is unrealistic to expect bootstrap values approaching 95%, the significance level usually used in statistics. Multivariate analyses were performed with the SPSSpc, the BMDP, and the PHYLIP computer programs.

Finally, to test the correspondence between nasal dimensions and temperatures, we have compiled information about monthly mean temperature for each Mongoloid population. With these data, a multiple regression analysis has been performed, considering alternatively the nasal height (NLH) and the nasal breadth (NLB) as the independent variable. With this analysis, it is possible to know which groups are the main outliers of the regression model by estimating the standardized residuals, defined as the differences between the observed values and those predicted by the model divided by the sample standard deviation of the residuals (Norusis, 1988).

TABLE 4. Analysis of variance and t*-test between each pair of Fueguian groups*[1]

	Males				Females			
	D.F.	F ratio	*P*	t	D.F.	F ratio	*P*	t
GOL	106	8.629	0.0003	b	70	11.247	0.0001	b,c
BNL	104	0.557	0.5746		66	3.247	0.0454	
BBH	103	0.879	0.4180		64	1.348	0.2670	
XCB	106	0.256	0.7746		66	1.157	0.3207	
XFB	102	0.706	0.4957		66	1.510	0.2287	
ZYB	95	1.267	0.2864		60	7.365	0.0014	b,c
AUB	104	13.408	0.0000	b	64	13.521	0.0000	b
ASB	103	0.670	0.5137		65	0.700	0.5001	
BPL	102	0.152	0.8587		64	0.647	0.5269	
NPH	104	6.557	0.0021	b	67	12.281	0.0000	b,c
NLH	104	2.741	0.0693		67	6.503	0.0027	b,c
OBH	106	0.382	0.6831		68	0.922	0.4024	
NLB	104	1.800	0.1705		66	1.743	0.1831	
MAB	101	0.390	0.6775		65	1.775	0.1777	
ZMB	99	2.193	0.1171		67	8.674	0.0005	b,c
SSS	97	1.584	0.2103		67	1.328	0.2720	
FMB	102	9.128	0.0002	b	66	4.592	0.0137	b
NAS	102	0.607	0.5466		66	1.383	0.2581	
EKB	97	3.093	0.0499		66	2.014	0.1418	
IML	101	0.997	0.3723		63	0.895	0.4136	
WMH	105	1.180	0.3112		67	4.450	0.0154	b
FRC	104	5.922	0.0037	b, c	70	5.740	0.0050	b
PAC	103	6.040	0.0033	a,b	70	4.341	0.0168	b
OCC	98	2.438	0.0927		67	0.568	0.5689	

[1] t, significant differences at 0.05 level between groups; a, Yámana-Kawéskar; b, Yámana-Selk'nam; c, Kawéskar-Selk'nam.

RESULTS

Results of the analysis of variance and the *t*-tests are given in Table 4. In both sexes, Selk'nam and Yámana are the most different groups, differing significantly in 6 of 24 variables in males and 10 of 24 in females. In males, Selk'nam and Kawéskar and Yámana and Kawéskar differ on one variable only. In females, no variable shows significant differences between the two canoeing groups (Kawéskar and Yámana), while Selk'nam and Kawéskar differ in five variables. However, the female Kawéskar sample is very small, and thus some comparisons must be viewed cautiously.

The results of the analysis of variance show that the terrestrial hunters from Isla Grande (the Selk'nams) can be differentiated from the canoeing tribes (Yámana and Kawéskar), more so in relation to the Yámana than the Kawéskar and more so in the case of females than males. In addition, a greater homogeneity exists between the two canoeing groups than within all the Fueguian sample, as expected from adaptation to a similar way of life. However, all three Fueguian groups share a general mor-

TABLE 5. Eigenvalues and PC scores obtained in the PCA analysis from the male and female Mogoloid samples

PCA (males)				PCA (females)			
Factor	Eigenvalue	Percentage of variable	Cumulative percentage	Factor	Eigenvalue	Percentage of variable	Cumulative percentage
1	10.46012	43.6	43.6	1	10.04965	41.9	41.9
2	4.79489	20.0	63.6	2	5.27605	22.0	63.9
3	2.63026	11.0	74.5	3	2.74972	11.5	75.3
4	1.37915	5.7	80.3	4	1.59393	6.6	82.0
5	1.27837	5.3	85.6	5	1.05013	4.4	86.3

	Male sample			Female sample		
Group	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3
ESK	0.392	0.770	−0.203	0.549	0.799	−0.205
ARI	0.019	−0.641	−1.161	0.003	−0.712	−0.852
YAM	0.629	−0.045	−1.144	0.473	0.303	−1.044
KAW	0.759	0.164	−0.969	0.287	−0.069	−1.527
SEL	1.337	0.004	−1.137	2.003	−0.003	−0.739
PER	−1.452	−0.548	−0.861	−1.490	−1.009	−0.506
BUR	1.625	−2.976	1.548	1.258	−2.526	1.351
MOK	0.546	0.813	0.702	0.232	0.955	1.027
EAS	0.431	2.258	0.629	−0.257	2.367	0.481
MOR	0.883	0.655	−1.082	0.808	0.494	−0.737
CAL	−0.447	−0.977	−1.600	−0.755	−0.514	−1.675
HOK	−0.465	−0.143	0.504	−0.824	−0.399	0.392
KYU	−0.888	0.403	0.441	−0.861	−0.055	0.592
HAI	−1.130	−0.187	0.289	−0.631	−0.153	1.456
TAI	−1.953	−0.285	0.035	−1.885	−0.005	0.093
PHI	−1.190	−0.119	0.448	—	—	—
GUA	1.011	0.476	0.760	0.912	0.195	1.198
AIN	0.358	0.357	1.206	0.177	0.333	0.694
ANY	−0.471	0.021	1.597	—	—	—

phological pattern that is very distinct from that of other Amerindian groups (Stewart and Newman, 1950; Lahr, 1995) and points to a single ancestral origin for all the Fueguian aborigines.

When comparing Fueguians with Howells's Mongoloid series, the principal component analysis yields very similar results in both sexes. In males, the first two factors account for 63.6% of the total variation (43.6 and 20.0%, respectively), while in females the value is 63.8% (41.9 and 21.9%, respectively) (Table 5). In both cases, the first factor is mainly correlated with some breadths and heights of the skull (glabello-occipital length (GOL), bizygomatic breadth (ZYB), biauricular breadth (AUB), nasion-prosthion height (NPH), nasal height (NLH), basion-prosthion length (BPL), biorbital breadth (EKB), nasion-bregma chord (FRC), inferior malar length (IML), and cheek height [WMH]). The second factor is dominated by few specific variables, mainly maximum cranial breadth (XCB) and maximum frontal breadth (XFB) (both in negative sense) and basi-bregma height (BBH) and bregma-lambda chord (PAC) (both in positive sense). The third factor, which explains 11% of the variation in males and 11.5% in females (Table 5), is mainly correlated with the nasal breadth (NLB) and also differentiates the southeast Mongoloids from the remaining populations. Both principal component analyses (Figs. 2, 3) show that a Mongoloid cranial pattern that is shared by East Asians (KYU, TAI, PHI, HAI, HOK, and ANY) and Amerinds (PER, CAL, and ARI) exists, while geographically marginal populations both in Asia and America have a more diverse morphology. Among these, we can include Pacific groups (EAS, MOK, GUA, and MOR), arctic groups (ESK and BUR), the Ainu (AIN), and the Fueguians (SEL, YAM, and KAW). With the exception of Buriats (BUR) and Easter Islanders (EAS), these geographically marginal populations are separated mainly by the first principal component, as a consequence of having larger cranial dimensions over many variables. The morphological traits of Mongoloid outliers may arise as a balance between in situ environmental adaptation and evolutionary

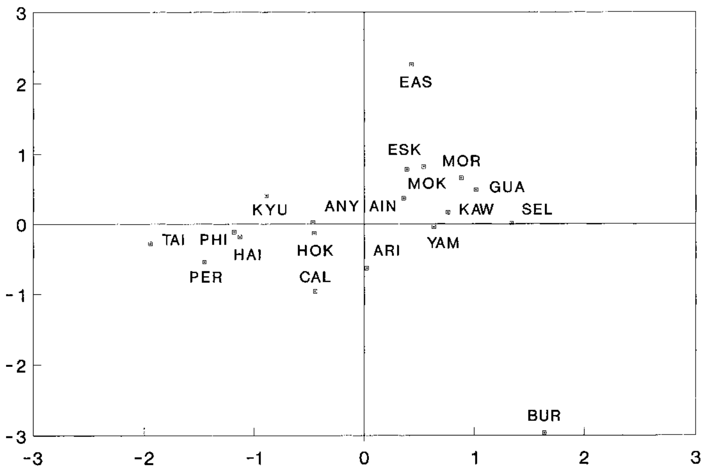

Fig. 2. Plot of factor 1 (horizontal axis) and 2 (vertical axis) of the principal component analysis generated from the male craniometric data, considering only Mongoloid populations. AIN, Ainu; ANY, Anyang; ARI, Arikara; BUR, Buriat; CAL, Santa Cruz; EAS, Easter Island; ESK, Eskimo; GUA, Guam; HAI, Chinese; HOK, Hokkaido; KAW, Kawéskar; KYU, Kyushu; MOK, Mokapu; MOR, Moriori; PER, Peru; PHI, Philippine; SEL, Selk'nam; TAI, Atayal; YAM, Yámana.

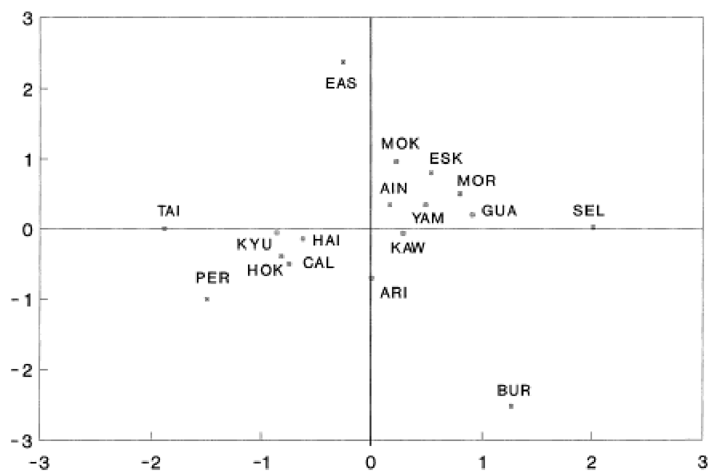

Fig. 3. Plot of factor 1 (horizontal axis) and 2 (vertical axis) of the principal component analysis generated from the female craniometric data, considering only Mongoloid populations. Abbreviations as in Fig. 2.

particularities arising from isolation and drift processes. The position of the Fueguian populations at the right in the first factor (Figs. 2, 3) shows that these populations are among those with highest craniofacial dimensions. Especially remarkable is the differentiation of the Selk'nam females, who probably had the most robustly built skull of the world's female populations. This special position among the female samples is mainly due to the low degree of sexual dimorphism showed by this group, a fact that still needs to be explained.

From the principal component analyses, it seems that a relatively high nasal height is a character shared by most of the Mongoloid groups, although it decreases from north to south in Asia. This is not surprising, when it is considered that the Mongoloid face has been explained as an ancestral adaption to cold (Coon et al., 1950). However, even if we allow this possible phyletic component to underlie morphology, nasal dimensions are important traits for differentiating Fueguian groups. When nasal height and breadth in all of Howells's series (including non-Mongoloid groups) are examined, we observe a wide range of nasal morphological patterns (Figs. 4, 5). The Fueguians and the Eskimos are the human groups with the narrowest and highest nasal apertures, displaying a combination of large nasal height and low nasal breadth values, while groups from equatorial areas have low, wide nasal apertures. Mongoloid groups from South Asia and the Pacific also have large nasal

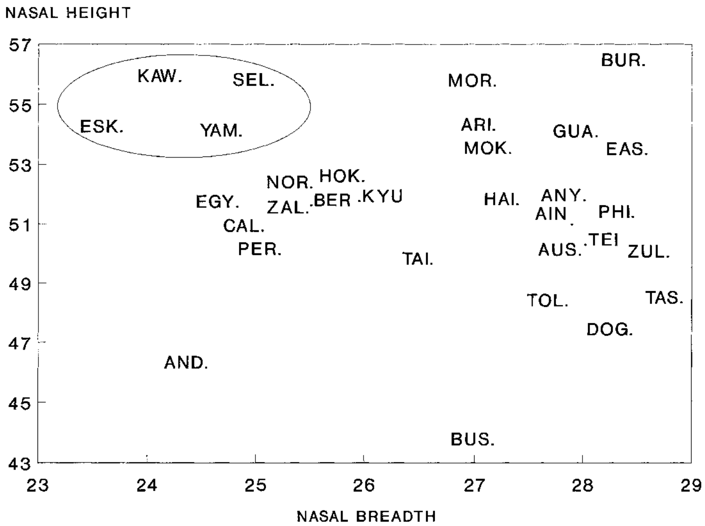

Fig. 4. Plot of nasal height (vertical axis) and nasal breadth (horizontal axis) for the male samples of Howells series. Circle includes the human groups (Eskimos and Fueguians) that lived in cold environments. Abbreviations as in Fig. 2. Also, BER, Berg; BUS, bushmen; DOG, Dogon; EGY, Egypt; NOR, Norse; TEI, Teita; ZAL, Zalavar; ZUL, Zulu.

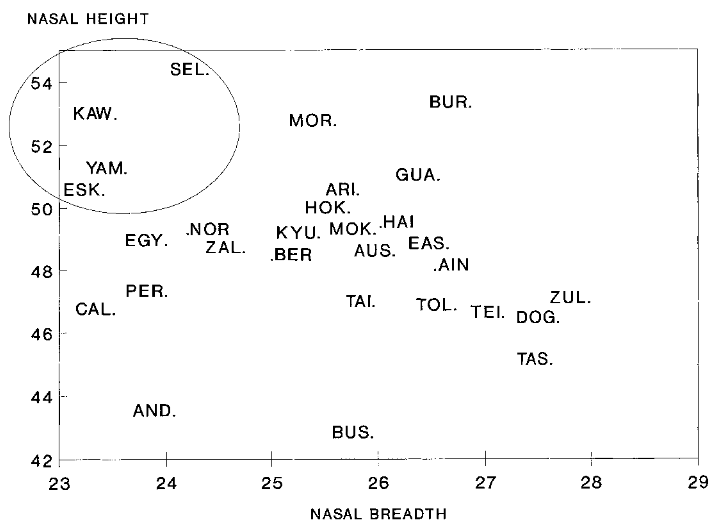

Fig. 5. Plot of nasal height (vertical axis) and nasal breadth (horizontal axis) for the female samples of Howells series. Circle includes the human groups (Eskimos and Fueguians) that lived in cold environments. Abbreviations in as Figs. 2 and 4.

heights, but they are combined with large values of nasal breadth. The Buriats, which have both large nasal breadth and length, are the northern exception to this morphological pattern.

Multiple regression analyses suggest that a general relationship exists between nasal dimensions and temperature, especially with respect to nasal height. When nasal height was the dependent variable, the coefficient of determination (R^2) was 0.958 ($F = 7.557$, $P = 0.033$). When nasal breadth was examined, no significant relationship to temperature was obtained ($R^2 = 0.848$, $F = 1.854$, $P = 0.290$). Thus, nasal height is more likely to reflect human adaptation to temperature. Also, because no standardized residual had an absolute value higher than three, the model does not have important population outliers (Norusis, 1988). In general, the Fueguian groups fit well within the theoretical model, although the Kawéskar have narrower noses than expected on the basis of temperatures in Tierra del Fuego (residual value of -1.326), while Selk'nams have larger nasal height values (residual of 1.033). In contrast, the Ainu tend to have shorter noses than previously expected (residual of

−1.065). These individual discrepancies are difficult to interpret because the regression analysis clearly represents an oversimplification of complex climatic conditions influencing adaption.

When we consider the whole Fueguian sample, the mean value of nasal height (NLH) is 54.99 (S.D. = 3.46; N = 107) for males and 52.13 (S.D. = 3.42; N = 70) for females, while for the three groups from North and South America (ARI, CAL, and PER) the mean value is 51.64 (S.D. = 3.01; N = 148) for males and 47.87 (S.D. = 2.64; N = 133) for females. Nasal height in non-Fueguian Americans is clearly lower (males: $t = 8.201$; females: $t = 9.789$; $P = 0.00$). It could be argued that the high nasal height in Fueguians is simply the reflection of high facial height. Both variables are tightly correlated, with a correlation coefficient of 0.839 ($P < 0.01$) in males and 0.876 in females of the Howells data set. However, the same argument can also be reversed, and high facial height could be the consequence of an adaptation operating through nasal height modification.

In the UPGMA analysis on the American male populations (Fig. 6), the morphological relationships among these groups became apparent. Groups are not arranged by geographical proximity but by climatic biotype. Despite their geographic distance, Fueguians and Eskimos form a single morphological cluster, while the remaining populations from North and South America (ARI, CAL, and PER) are grouped together. The values of the bootstrap analysis, displayed at the nodes as percentiles, provide support for these cranial affinities. Especially robust is the clustering of the three Fueguian tribes and, separately, that of the PER and CAL samples, showing values of 84% and 85%, respectively. In contrast, the grouping of Eskimos with the three Amerind groups (ARI, CAL, and PER) does not occur in the bootstrap results, and the clustering of each Fueguian group with the Amerind groups has values that range only from 0–1%. The UPGMA tree obtained with the female samples has a similar topology (data not shown), although the bootstrap values are slightly smaller than those observed in the male tree. Fueguians and Eskimos are

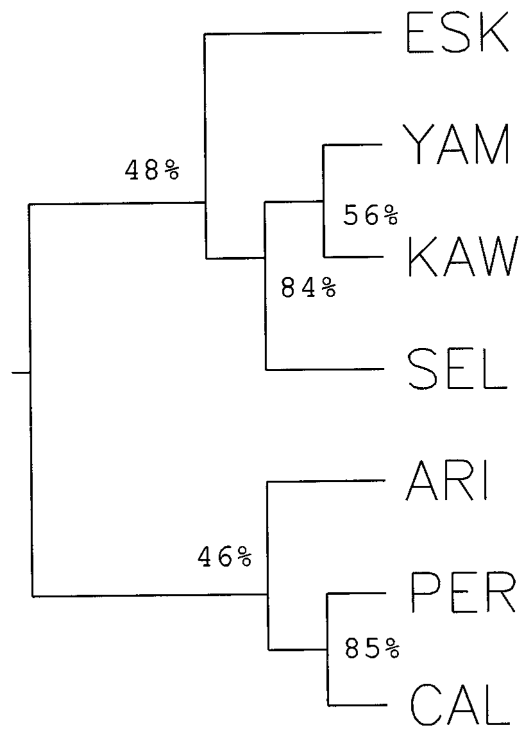

Fig. 6. Average linkage phenogram (UPGMA) based on the squared Euclidean distance for the male American samples. Percentages indicate the frequency of each branch among 100 bootstrapped trees. Abbreviations are defined in Fig. 2.

grouped in a cluster in 35% of the bootstraped trees, while the Fueguian cluster shows values of 38%. In 24% of cases, however, the Selk'nam form a separate branch. This discrepancy is due to the notable cranial robusticity of the Selk'nam females.

As the Amerindian groups (ARI, CAL, and PER) inhabited temperate or hot climates and the Fueguians and Eskimos were in colder ones, it can be hypothesized that climatic adaptation made the two main branches of the tree more similar through those traits that respond adaptively to climate.

DISCUSSION

Nasal form

Several morphological traits of the skull are thought to have been influenced to some extent by the environment. The extremely flattened faces that characterize the Mongoloid group but especially northeast Asians

and arctic peoples such as the Yukagirs, the Yakuts, the Chukchis, or the Eskimos, have been explained as adaptations to an extremely cold environment (Coon et al., 1950). However, some experimental studies (Steegman, 1975) and the finding that midfacial flatness in Eskimos increases with age (Dahlberg et al., 1978) do not support the hypothesis of cold facial adaptation. Also, some Eskimo populations resemble northern North American Indians in their craniofacial dimensions, even in facial flatness. Szathmary (1979) reported that Western Alaska and Saint Lawrence Island Eskimos show morphological affinities with Athapaskan Indians, while Caribou Eskimos are morphologically close to the Cree Indians. However, a possible adaptation to cold in subarctic Athapaskan Indians could also explain these relationships, although this is an issue that remains to be studied (Szathmary, 1984).

Nose form has been associated with climatic factors due to its functional relationship with thermoregulation (Weiner, 1954; Steegman, 1975; Crognier, 1981; Franciscus and Long, 1991). In this sense, the extremely high and narrow nose of the Eskimos, characterized by the “pinched-up” appearance of the nasal bones (Collins, 1951) and an expanded interior nasal chamber (Shea, 1977), has been regarded as an adaptation to cold and dry environment (Newman, 1953; Garn, 1965; Wolpoff, 1968). Although it is not well understood how nasal dimensions are correlated with differences in the physiology of respiration (Dean, 1988; Wheeler, 1990), it seems that a high, narrow nose contributes to warm, moister inspired air and to the recovery of heat and moisture from expired air (Weiner, 1954; Franciscus and Long, 1991). Nasal form in Neanderthals has also been interpreted as an adaptation to cold by several authors (Coon, 1962; Schwartz and Tattersall, 1996). In this case, as the plesiomorphic condition in early Middle Pleistocene was a very wide nasal aperture, the selective forces might have built a facial morphology that differs from that observed in modern human groups adapted to cold.

However, the cold-adapted feature of the human cranium is not necessarily represented by nasal shape and facial flatness only. Climatic conditions can also influence many other aspects of head shape and cranial morphology (Hiernaux and Froment, 1976; Guglielmino-Matessi et al., 1979; Beals et al., 1984). It has been suggested that a rounded head (brachicephaly) tends to preserve more the heat than an elongated head (dolichocephaly). However, some Eskimo groups are notably dolichocephalic (Harrison et al., 1964), and thus this hypothesis is debatable as a general rule. Also, as dolichocephaly was the common condition in Pleistocene crania, it is not surprising that Fueguians had long heads.

Head shape has also been found to correlate with tooth size and masticatory muscle strength. The temporal and masseters muscles are related to measures of facial width (Weijs and Hillen, 1986). In fact, Eskimo craniofacial morphology has also been interpreted as a result of high masticatory stress through the adaptation to hard chewing (Hylander, 1977). Lahr (1995) suggests that morphological similarities shared by Eskimos and Fueguians are mainly due to similar conditions of biomechanical stress. However, our results show that Fueguians and Eskimos have a very similar nasal morphology, a cranial structure that a priori seems to be little affected by mastication biomechanics. It can be debated whether an enlargement of the frontal processes of the maxillae is an efficient biomechanical adaptation that transfers large biting forces from the anterior teeth to the neurocranium, as Hylander (1977) suggested. Our results show that Fueguians and Eskimos present a pattern of higher and narrower nasal apertures than those observed in other human populations, despite some minor morphological particularities. From our point of view, when adaptation occurs, it involves the modification of the available structures, and thus adaptation to similar climatic conditions should not necessarily result in the same anatomical details. Moreover, Fueguians and Eskimos are among the few groups that ever inhabited areas beyond 53° of latitude S and 70° of latitude N, respectively, a geographic variable intercorrelated with a number of climatic conditions but mainly temperature and humidity.

In conclusion, although the adaptiveness of craniofacial structures in Eskimos and arctic groups is a matter of controversy, we consider that climate adaptation is still the most plausible interpretation of the widely reported association between nasal form and temperature. In this context, the relationship of the nasal form in Fueguians with cold climatic conditions seems consistent.

Paleo-Indian samples

Due to the long-standing isolation of Fueguians, Paleo-Indian remains probably constitute the best sample for comparison with Fueguian aborigines, if one wishes to define their morphological particularities. Unfortunately, the Paleo-Indian sample is rather small, disperse, and fragmentary at present (Steele and Powell, 1992; Neves and Pucciarelli, 1991). However, we do know that Paleo-Indians have a shorter and narrower face than that observed in present-day North American Indians and Northern Asians. This has been interpreted as an evidence of a later migration into Americas of individuals with more "typical" Mongoloid features (e.g., broad and flat face and sinodont dentition) (Steele and Powell, 1992; Lahr, 1995).

If Fueguians developed cranial features adapted to cold, these might have been developed from preexisting craniofacial structures of Paleo-Indians. Accordingly, the fact that Paleo-Indians did not possess the typical flat face of the northeast Asians (Steele and Powell, 1992) allows the possibility that the adaptation to cold in Fueguians produced a morphological pattern distinct from that observed in arctic peoples.

On the other hand, Paleo-Indian skeletal samples show a nasal height (NLH) similar to that observed in present-day populations from continental Americas. The values of NLH in these samples are 48.5 (N = 8, from Lagoa Santa, Sumidouro, Brasil), 51.0 (N = 6, Lagoa Santa, Composite, Brasil) and 50.0 (N = 5, Tequendama, Colombia), with dates for the samples ranging from 12,000 to 6,000 years BP (Neves and Pucciarelli, 1991). Data on Paleo-Indian specimens from North America, dated to 8,500 years BP or older, are also similar, with an NLH mean value of 51.0 (N = 10) (Steele and Powell, 1992). This supports the hypothesis of a posterior modification of nasal height through climatic pressures on isolated Fueguians.

Physiological adaptations

Climatic conditions seem to have strong effects on the body size and shape of human populations, perhaps as a reflection of thermorregulatory mechanisms. However, culture acts as a powerful buffer against environment in many human groups. For example, arctic peoples use clothing and other cultural adjustments to prevent exposure of the body to cold.

In contrast, the three tribes of Fueguians have been described as almost naked throughout their lives. It could be expected that selective pressures over the general phenotype might have been important to these individuals. At present, little information is available on body size and form in Fueguians (Gusinde 1939, Varela et al., 1993–1994).

Some ethnological studies indicate that Fueguians had effectively developed important physiological adaptations to continual cold exposure, such as a thick, subcutaneous deposit of fat, high basal metabolic rates, and high body temperature (Hammel, 1960, 1964). Other special adaptations related to a highly carnivorous diet in these groups could have included a distinct metabolic control of fat (Nardi, 1977), which they consumed in large quantities (Hyades and Deniker, 1891; Martial, 1888; Gusinde, 1951). However, a high fat diet can involve physiological modifications that do not correspond to biological adaption. Unfortunately, as Fueguians are extinct, it is not possible to determine the existence of a real biological adaption in these groups.

Biomechanical stress

The hypothesis of adaptation to cold does not exclude the possibility that other morphological characteristics of Fueguians, especially their unusual degree of cranial robustness and some aspects of craniofacial width, could be due to a large masticatory stress (Gusinde, 1939; Lahr, 1995). Morphological complexes related both to mastication and respiration vary considerably with climate, and thus they can be indirectly correlated. Several ethnological studies in Fueguians

described the use of the mouth as a third hand for working with skins, leather strips, wood, or bone, shaping lithic instruments, and opening shells (Hyades and Deniker, 1891; Lothrop, 1928; Gusinde, 1939). The extensive use of teeth as a tool is consistent with the high degree of dental wear described in Fueguian remains (Kozameh, 1993), similar to that observed in Eskimos (Pedersen, 1952; Hart Hensen et al., 1991).

Eskimos and Fueguians were probably subjected to similar levels of facial biomechanical stress as a consequence of the continuous and close interaction of these individuals with their environment. In fact, some variables that show extreme values in the Fueguians, such as bizygomatic breadth (ZYB), biauricular breadth (AUB), bifrontal breadth (FMB) or cheek height (WMH), can be interpreted as a response to large biomechanical stress. However, it is difficult to elucidate whether some traits of cranial robustness are simply the retention of plesiomorphic features due to the isolation of these groups (phyletic hypothesis) (Lahr, 1995) or if it is a secondary characteristic arising from adaptation to severe environmental conditions (environmental hypothesis). Study of a larger sample of Paleo-Indians skulls than is currently available is needed to obtain additional information about this dichotomy.

Genetic evidence of Fueguian origins

Ancient DNA studies (Lalueza, 1995, 1996a) have demonstrated that Fueguians cluster within two of the major mitochondrial lineages extensively described in Amerindian populations (Torroni et al., 1993; Merriwether et al., 1995) and thus show a reduced mitochondrial genetic diversity. From the 60 individuals successfully analyzed (Lalueza 1996a), 59 belong to two of these haplogroups, C and D, lacking the B and A lineages; a remaining individual does not fit in any of the four major lineages, as observed in other American groups (Merriwether et al., 1995). The presence of C and D mtDNA lineages in Fuego/Patagonia must be interpreted in the context of the general clinal pattern observed in the Americas (Lalueza, 1996b). While the A haplogroup shows a continuous north-to-south decrease, the B haplogroup does not follow any clear latitudinal pattern, being absent in both northern and southern extremes of the Americas.

In the context of a continental clinal pattern, the loss of haplogroup A in Fueguians can be attributed to the effect of drift (Lalueza, 1996a). However, its simultaneous absence in three groups that were fairly isolated among them constitutes additional support for an ancestral common origin. In addition, the analyses of the last 10 Yámana survivors (Llop et al., 1995; Merriwether et al., 1995) and the blood group results in 34 surviving individuals (Lipszchutz et al., 1946) also point to a relative genetic uniformity in all Fueguian groups. Furthermore, the genetic results from Fuego/Patagonia are in agreement with the American mitochondrial pattern, proving that these groups, despite their cranial particularities, were effectively Amerindians.

CONCLUSIONS

From our point of view, the distinct morphological pattern of Fueguians can be regarded as the consequence of both climatic and biomechanic adaptations, with independent retention of features that are common in Pleistocene crania. Under the climatic circumstances of Tierra del Fuego and the long-standing isolation of these groups, it is reasonable to expect the development of adaptations to a cold environment. The naked lifestyle of Fueguians might be related to the existence of morphological and physiological adaptions more appropriate against cold stress than cultural adjustments, since Tierra del Fuego land was poor in environmental resources. Moreover, assuming an initial entry in Tierra de Fuego of around 10,000 BP, a systematic adaptive pattern to cold stress might be the reflection of only 8,000–10,000 years' development. Our hypothesis is that, under harsh environmental conditions like those present in Tierra del Fuego, the rate of the morphological change of human populations can be notably increased. The geographic isolation of these groups may have contributed to the maintenance of a general morphological homogeneity within the Fueguian samples, despite the development of reliable differences at-

tributable to differences in the way of life among these groups. The final conclusion is that these human groups were well adapted to their extreme environment from a cultural, morphological, and physiological point of view.

ACKNOWLEDGMENTS

We express our gratitude to M. Mirazón Lahr and one anonymous referee for their helpful comments and suggestions and also to the different curators of the American and European institutions visited for allowing us access to Fueguian skull collections.

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